J. New York Entomol. Soc. 102(2):127–141, 1994

RECOGNITION OF THE WEST ASIAN *ANCHOMENUS KURNAKOVI* AND *A. PUNCTIBASIS* (COLEOPTERA: CARABIDAE: PLATYNINI) AND MIOCENE EVOLUTION OF THE MEDITERRANEAN AND PARATETHYS SEAS

James K. Liebherr

Department of Entomology, Comstock Hall, Cornell University,
Ithaca, New York 14853-0901

Abstract.—The two Palaearctic species, *Agonum kurnakovi* Kryzhanovskij and *Agonum punctibasis* Reitter, are newly combined as members of the genus *Anchomenus* Bonelli. Descriptions, distributional data, and means to identify the species are presented. The species are included in a cladistic analysis with the other members of the *Anchomenus* clade; *Tetraleucus picticornis* Newman, 10 other species of *Anchomenus*, the 7 species of *Sericoda* Kirby, and the 11 species of *Elliptoleus* Bates. This analysis preserves relationships presented in Liebherr (1991) within and among the other three genera, but defines a new set of cladistic relationships within Old World *Anchomenus*. These relationships are used to define an area cladogram for the circum-Mediterranean region that is concordant with those of a variety of groups summarized by Oosterbroek and Arntzen (1992). Diversification of Palaearctic *Anchomenus* is explained in the context of geological evolution of the Mediterranean Sea during the Miocene.

The genus *Anchomenus* Bonelli is distributed across the Palaearctic Region, and in Vancouveran North America from Alaska to Baja California Sur (Liebherr, 1991). In that revision, I recognized six Old World species and four from the New World. Member taxa possess a characteristic female spermatheca, in which there is a basal reservoir and an apical filament, with the spermathecal gland duct entering the basal reservoir (e.g., Fig. 14). Externally, *Anchomenus* species exhibit a cordate pronotum (e.g., Figs. 9, 10), often with rugose laterobasal depressions; 1–6 anteroventral and 3–10 posteroventral setae on the profemur. Possession of the latter states of leg setation are synapomorphies at the generic level that distinguish *Anchomenus* from its sister group (=adelphotaxon of Ax, 1987) composed of the genera *Sericoda* + *Elliptoleus*; those genera sharing the synapomorphy of setose parameral apices in the male genitalia (Liebherr, 1991, fig, 292).

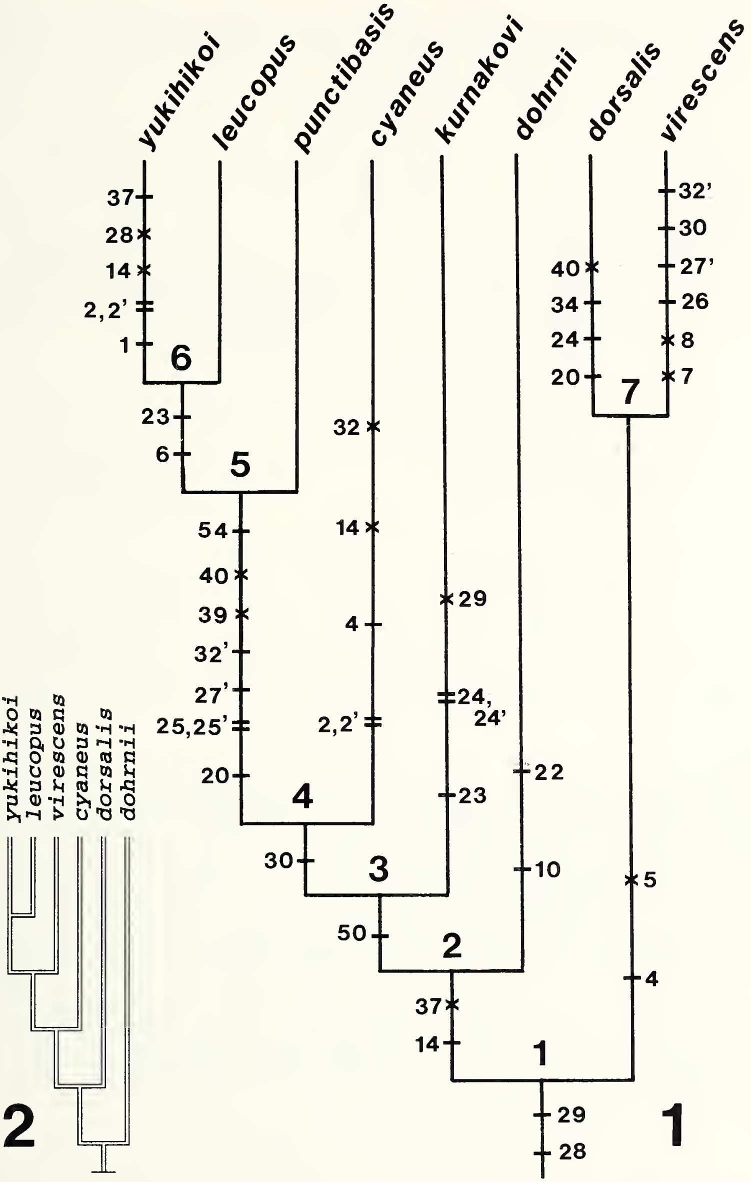
While conducting a survey of the over 130 species assignable to the Holarctically distributed genus *Agonum* Bonelli, I discovered that the West Asian species, *Agonum punctibasis* Reitter, exhibited a female spermatheca of the *Anchomenus* type. The configuration of leg setae also differed from that of *Agonum* species, which generally possess fewer femoral setae than *Anchomenus*. A thorough comparison of the characters exhibited by *A. punctibasis* convinced me that the species should be transferred to *Anchomenus*. At the same time, through the courtesy of Dr. O. L. Kryzhanovskij, I had the opportunity to borrow the paratype of *Agonum* (?*Anchodemus*) *kurnakovi* Kryzhanovskij. This single specimen available to me is a male. But, nonetheless, the characters of leg setation, pronotal shape and laterobasal depression rugosity, and male aedeagal configuration, convince me that this taxon should also be transferred to *Anchomenus*. This contribution formally combines these two species names with *Anchomenus*, and provides modifications to my key (Liebherr, 1991) to permit identification of them as members of the genus. I also examine how recognizing these taxa as members of *Anchomenus* requires reinterpretation of the area relationships defined in a cladistic biogeographic analysis for the genus. The new area cladogram based on the eight Palaearctic *Anchomenus* is concordant with those summarized by Oosterbroek and Arntzen (1992) for a variety of circum-Mediterranean taxa. Speciation events in the Palaearctic *Anchomenus* can be accounted for by the successive vicariance and fusion of European and West Asian areas bordering the northern shores of the Mediterranean and Paratethys Seas during the Miocene.

MATERIALS AND METHODS

Taxonomic, cladistic, and biogeographic methods are those of Liebherr (1991). I have examined additional taxonomic material from the following institutions through the courtesy of their curators: Academy of Sciences, St. Petersburg, Russia (ASSP), O. L. Kryzhanovskij; B. P. Bishop Museum, Honolulu (BPBM), G. A. Samuelson; Hungarian Natural History Museum, Budapest (MNHB), G. Szél; Museum National d'Histoire Naturelle, Paris (MNHP), T. Deuve; Zoologische Staatssammlung, Munich (ZSSM), M. Baehr; and Dremm-Mab Morvan personal collection, Bretagne (DMMC).

CLADISTIC ANALYSIS

The two additional species were coded for the same characters included in the cladistic analysis of Liebherr (1991), with no new shared-derived characters—i.e., potential synapomorphies—found. *A. kurnakovi* possesses the derived states for the following characters (states described in Liebherr, 1991, pp. 116–118; state 1 unless noted in parentheses): 5, 14, 23, 24(2), 27, 28, 32, 39, 40, 50. *A. punctibasis* exhibits the derived states for the following: 5, 14, 20, 25(2), 27(2), 28, 29, 30, 32(2), 50, 54. I was not able to examine the female holotype of *A. kurnakovi*, and thus could not score the characters of the female reproductive tract (41–46). Scoring these characters as unknowns (? in HENNIG86, Farris, 1988) results in identical relationships within *Anchomenus* as presented below, but changes optimizations lower on the cladogram. This causes the rendering of *Sericoda* into a paraphyletic group, with the Holarctic *S. quadripunctata* DeGeer and the Himalayan *S. lissoptera* Chaudoir as secondary and primary outgroups to the Mexican *Elliptoleus* (see Liebherr, 1991, fig. 292). Accepting this solution amounts to basing classificatory changes in one clade strictly on lack of information in its adelphotaxon. Moreover, in this case, acceptance discounts metacoxal setation as the basis for monophyly of *Sericoda* (Liebherr, 1991, fig. 292, character 26), even though this character is relatively nonhomoplasious across the *Anchomenus* clade. Instead, as placement of *A. kurnakovi* within *Anchomenus* is supported on other characters—leg setation, pronotal shape, and male aedeagal configuration—and because other *Anchomenus* species exhibit the plesiomorphic state for all female characters, those plesiomorphic states were assumed for *A. kurnakovi*.



Figs. 1, 2. Taxon cladograms for Palaearctic species of *Anchomenus*. 1. Cladistic relationships of 8 currently recognized species. Character-state advances shown by hash marks, reversals by ×'s; synapomorphies outside this clade not shown (see Liebherr, 1991, fig. 292); character numbers correspond to Liebherr (1991, pp. 116–118); cladogram node numbers referenced in text. 2. Topology of taxon cladogram including the 6 species recognized in Liebherr (1991).

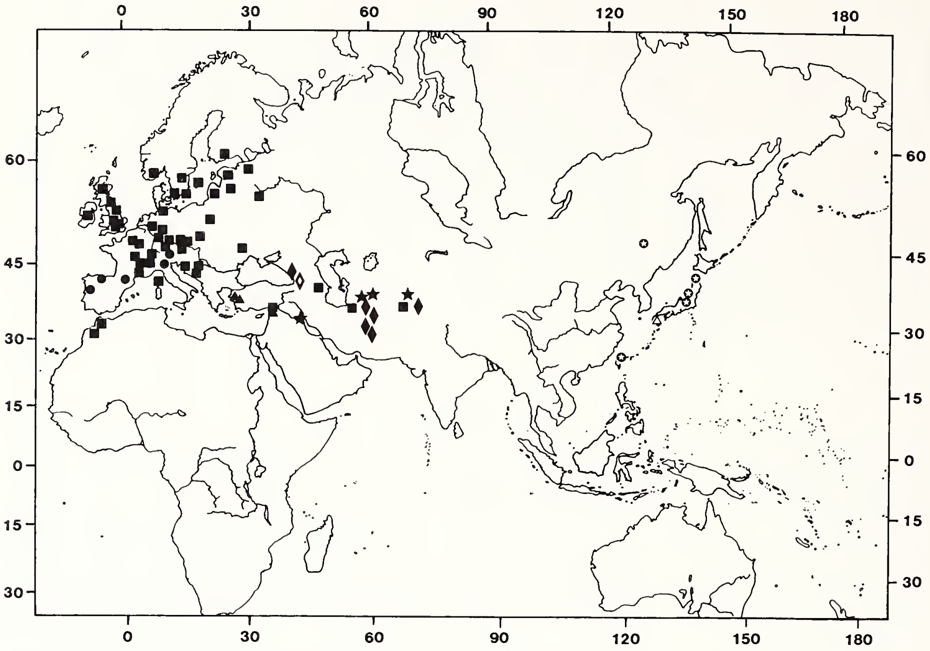


Fig. 3. Distributions of Palaearctic species of *Anchomenus*. ● = *A. cyaneus*, ▲ = *S. dohrnii*, ■ = *A. dorsalis*, ◇ = *A. kurnakovi*, ✪ = *A. leucopus*, ◆ = *A. punctibasis*, ★ = *A. virescens*, △ = *A. yukihikoi*.

Cladistic analysis using HENNIG86 (Farris, 1988), starting the analysis using the m, m*, h, h*, and tread commands to search for islands of equally parsimonious trees (Maddison, 1991), resulted in the discovery of 4 equally parsimonious trees of step length 172, consistency index 0.37, and retention index 0.69. These were summarized using strict consensus, or the nelsen option. This consensus tree is identical to that of Liebherr (1991, fig. 292), except within the clade of Palaearctic *Anchomenus* (Fig. 1). Within the Old World species, the inclusion of two additional species results in retention of only the adelphotaxon relationship of *A. leucopus* Bates and *A. yukihikoi* Habu (Fig. 2). Based on the new evidence, it is most parsimonious to propose *A. dorsalis* Pontoppidan and *A. virescens* Motschulsky as sister species, and the other six species as their adelphotaxon.

BIOGEOGRAPHIC ANALYSIS

Both *A. punctibasis* and *A. kurnakovi* are distributed in West Asia (Fig. 3). *A. kurnakovi* is known only from the type locality in the Georgian Adzharo-Imeritinsky Mountains. *A. punctibasis* is more widely distributed, mostly found east of the Caspian Sea in Iran, Tadzhikistan and Turkmenistan, but with one record in Georgia, from Abkhazia.

If we recognize areas of endemism for this analysis based on species distributions, with the smallest distributions defining areas (Fig. 4), we must add one area (area J')

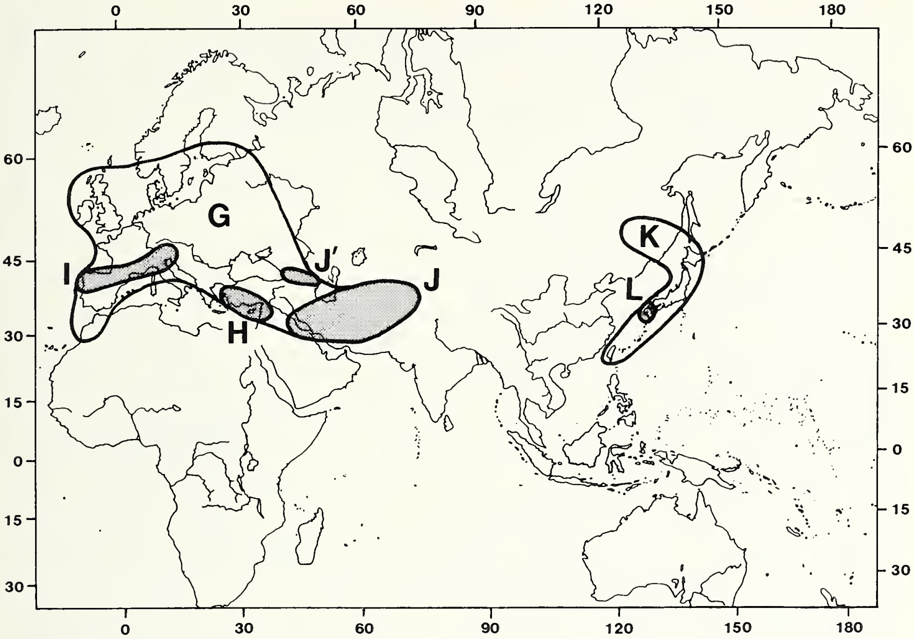
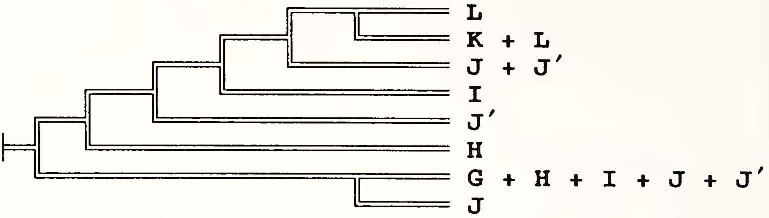


Fig. 4. Areas of endemism defined by species distributions of Fig. 3 (see text).

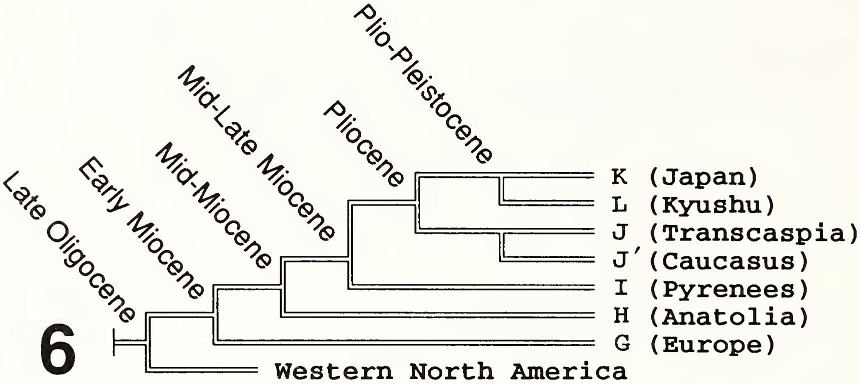
to those previously recognized (Liebherr, 1991). In this analysis, area G represents the areas in which the widespread *A. dorsalis* occurs allopatric relative to other *Anchomenus*. In smaller areas around the periphery of the range of *A. dorsalis*, this species is sympatric with *A. dohrnii* (area H, in mountainous Anatolia), *A. cyaneus* (area I, the Pyrenees and Alps), *A. virescens* (area J, mountainous Transcaspia), and *A. kurnakovi* (area J′, the Caucasus mountains). From East Asia, the range of the geographically restricted *A. yukihikoi* (area L, Kyushu) is surrounded by the range of its adelphotaxon, *A. leucopus* (areas K + L, Japanese archipelago, Formosa, and Manchuria).

The taxon cladogram (Fig. 1) was converted to a taxon-area cladogram (Fig. 5), with the taxon-area cladogram used to define a fundamental area cladogram in which each area was represented once (Fig. 6). In this analysis, Assumption 0 (Page, 1990) as implemented in the COMPONENT program (Page, 1989) was used to derive a single fundamental area cladogram, meaning that species occupying more than one area supported a most recent historical connection among those areas. Analyses were also attempted using conditions of Assumptions 1 and 2, however the program bombed when 1,190 and 1,142 equally parsimonious trees respectively consumed the program's memory.

The fundamental area cladogram derived under Assumption 0 is characterized by a progressive fragmentation of the Palaearctic from west to east. The vast expanse of northwest Europe is first separated from Anatolia, the southerly Alps and Pyrenees, the mountains of West Asia, and East Asia. The Anatolian region is next isolated, 5



6



Figs. 5, 6. 5. Taxon-area cladogram summarizing species' cladistic relationships and distributions. 6. Fundamental area cladogram derived from taxon-area cladogram using Assumption 0. North American *Anchomenus* comprise adelphotaxon to Palaearctic clade, with Oligocene trans-Beringean vicariance consistent with Allen (1983) and Tangelder (1988). Timing of Palaearctic divergence events derived from geological model (Fig. 7) in concert with taxon cladogram (Fig. 1).

then the Pyrenees and Alps. Finally, the easterly areas surrounding the Caspian Sea are vicariated from the distant Japanese archipelago in East Asia. The final pair of vicariance events includes isolation of Kyushu from the rest of Japan, Formosa, and mainland north China, and vicariance of mountain habitats in Georgia versus Transcaspia. This westerly to easterly vicariance sequence within the Mediterranean region was found to be a general pattern for a number of circum-Mediterranean taxa reviewed by Oosterbroek and Arntzen (1992). Taxa summarized in their paper include *Nephrotoma* and the *Tipula* (*Acutipalpa*) *maxima* group of the Tipulidae, the *Rana ribicunda* and *Rana temporaria* groups (Anura: Ranidae), and the subgenera *Triturus* and *Palaeotriton* of *Triturus* (Urodela: Salamandridae). They proposed a scenario whereby the Balkans and Asia Minor were colonized from the main European land mass, either from the west or north, during Oligocene to early Miocene. This event would have occurred when the area to become Anatolia was connected to western Europe along the northern shore of the Mediterranean (Fig. 7A; Steininger and Rögl, 1984). Subsequent connection of Anatolia to Asia Minor, and vicariance between Anatolia and western Europe (Fig. 7B), followed by total isolation of Anatolia (Fig. 7C) permitted emergence of a Balkan fauna. In Mid-Miocene, this fauna spread throughout Europe when land connections were reinstated (Fig. 7D, E). The Caucasus

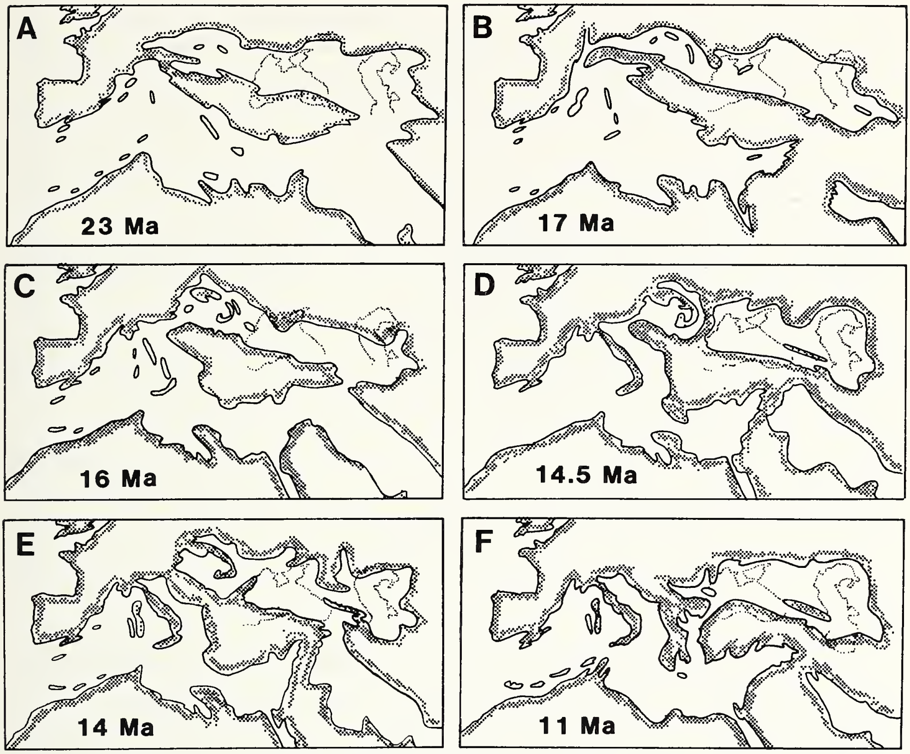


Fig. 7. Geological history of the Mediterranean region throughout the Miocene (redrawn from Steininger and Rögl, 1984). Land margins stippled; current Black and Caspian Sea margins shown by dotted lines; ages of land configurations shown in millions of years (Ma).

first emerged as a separate mountain range at this time, with isolation first about 14.5 Ma (Fig. 7D), and again in Late Miocene (Fig. 7F).

The fundamental area cladogram for Palaearctic *Anchomenus* (Fig. 6) is largely concordant with this scenario. The initial vicariance of European and Anatolian lineages (areas G, H, Fig. 6; Fig. 7A, B, C) was followed by dispersal into Europe by the Anatolian lineage when Anatolia was again contiguous with western Europe (Fig. 7D, E). This led to colonization of the Pyrenees and the Alps (Fig. 6, area I; Fig. 7E, F). The Pyrenees were formed by two bouts of orogeny, the first dated Paleocene to Eocene, the second in the Late Miocene, about 10 Ma (Plaziat, 1981; Oosterbroek and Arntzen, 1992). Given initial vicariance within this lineage at 23 Ma, or Early Miocene, only the second bout of Pyrenean orogeny figures in the isolation of populations comprising *Anchomenus* ancestors.

To the east, occupation of Anatolia could have permitted colonization of areas to the south of the present Caspian Sea as early as 17 Ma (Fig. 7B). Based on the fundamental area cladogram for *Anchomenus* (Fig. 6), these areas were not colonized until somewhat later, contemporaneous to dispersal westward to the proto-Alps and proto-Pyrenees (Fig. 7D, E). The Caucasus mountains were first isolated in Mid-Miocene (Fig. 7D), suggesting the earliest possible time of vicariance for the Caucasus and Transcaspia (areas J and J′, Fig. 6) relative to areas to the west (i.e., areas H, I, Fig. 6). If we assume isolation in the Pyrenees at 10 Ma, it is more logical to assume a later isolation of the Caucasus leading to present-day *Anchomenus* species; i.e., during the second bout of isolation and orogeny about 11 Ma (Fig. 7E). As noted below, this choice reflects discordance between the fundamental area cladogram, and a biogeographic scenario derived directly from the taxon cladogram.

The East Asian areas in China, Formosa, and the Japanese archipelago (areas K, L, Fig. 6) are most closely related to the areas surrounding the Caspian Sea (areas J, J′). Large tracts of non-forested steppe vegetation already occupied intermediate areas by the Pliocene (Frenzel, 1968), dating vicariance between the Japanese and Caspian areas from 10 to 3 Ma. Whether or not the large intermediate regions are currently inhospitable to *Anchomenus* remains a goal for future survey and study.

Finally, the two sister area relationships, J and J′, and K and L, can be dated as Pliocene to Pleistocene. During the Pleistocene glacial episodes, riparian vegetational belts connected the mountainous regions surrounding the Caspian Sea (Frenzel, 1968), and could have provided means to maintain connections among riparian *Anchomenus* in the region. These riparian belts were eliminated or moved northward during interglacial periods, affording the means to isolate populations on either side of this sea.

In Japan, the occurrence of *A. yukihikoi* at only the type locality on Kyushu, with its range in the midst of its adelphotaxon, *A. leucopus*, suggests speciation of the former via isolation of a peripheral population of their common ancestor.

Given the above scenario based on the fundamental area cladogram, and the geological history of the circum-Mediterranean region, the taxon cladogram (Fig. 1) can be reexamined, with tentative dates assigned to the various nodes. The initial vicariance (node 1) would be dated as early Miocene, resulting in the ancestor of *A. dorsalis* + *A. virescens* in northwest Europe, and the ancestor of *A. dohrnii* plus the rest of the species in Anatolia.

Differentiation within Anatolia proceeded by colonization of areas to the east, i.e., the Caucasus, leading to speciation of *A. kurnakovi* (node 3, Fig. 1). Based on the taxon cladogram, this event occurred after Anatolian isolation (Fig. 7C), but before evolution of the Pyrenees (Fig. 7F). However, based on the fundamental area cladogram (Fig. 6), isolation of the Caucasus occurred after development of the present-day Pyrenees and Alps. This tension can be resolved by recognizing that the general summary of all species information using Assumption 0 supports the later Caucasian vicariance, whereas the cladistic position of *A. kurnakovi* supports the earlier vicariance. Because of Assumption 0, the general summary is heavily influenced by the distribution of *A. punctibasis* in areas J and J′ (Figs. 1, 3, 5), and the adelphotaxon relationship of *A. punctibasis* versus *A. leucopus* + *A. yukihikoi* (Figs. 1, 5). As a means of resolution, it is suggested that *A. kurnakovi* was isolated in the Caucasus at Mid-Miocene (Fig. 7D), whereas *A. punctibasis* first occupied the area in Late Miocene (Fig. 7E).

Range expansion in Mid-Miocene (Fig. 7D, E) during orogeny of the present-day Pyrenees and Alps resulted in colonization of a large area of Europe and Asia, followed by speciation of *A. cyaneus* (node 4, Fig. 1). Isolation of the European mountain ranges from those east of the Bosporus (Fig. 7F) by Late Miocene formed the basis for the final diversification in Palaearctic *Anchomenus*. These events include Miocene to Pliocene vicariance of the Caucasian and Transcaspian regions from the coastal forests of China and Japan (Frenzel, 1968), resulting in speciation of *A. punctibasis* (node 5, Fig. 1).

Two final cladistic events include speciation of the East Asian *A. leucopus* and *A. yukihikoi* (node 6, Fig. 1), and the West Asian *A. virescens* and *A. dorsalis* (node 7, Fig. 1). Both sister-species pairs exhibit a pattern in which the range of the narrowly distributed species is within the range of its more widespread sister (Fig. 3), suggesting that speciation proceeded by isolation of peripheral populations followed by recolonization of the narrowly distributed species' range by the more widespread species, i.e., the centrifugal speciation model (Brown, 1957). Speciation of *A. leucopus* and *A. yukihikoi* likely occurred in Pliocene to Pleistocene, that age constrained by the time of origin of *A. punctibasis* (Fig. 1). Speciation of *A. dorsalis* and *A. virescens* may have occurred in the Pleistocene, Pliocene, or earlier. The timing of this event is not narrowly delimited by more basal cladistic relationships, as these two species form the sister group of the other six Palaearctic species. Separation of mixed conifer/deciduous forest in Europe versus the Caucasus, as observed at the end of the Pliocene (Frenzel, 1968, fig. 2), would have afforded the type of vegetation pattern likely to be associated with isolation of populations leading to speciation of *A. virescens*. Subsequent vegetational movements during the Pleistocene would have provided the means to reestablish sympatry between *A. dorsalis* and *A. virescens*.

This scenario provides much more specific conditions for diversification of Palaearctic *Anchomenus* than I previously proposed (Liebherr, 1991). Adoption of this scenario requires modification of timing for the origin of *Anchomenus* within the four-genus *Anchomenus* clade. I previously suggested that the Old World and New World *Anchomenus* were isolated by climatic cooling across Beringia in Mid- to Late Miocene (starting 12 Ma). The considerations of Palaearctic *Anchomenus* presented here suggest that this vicariance was older, perhaps as early as Late Oligocene (23–24 Ma). Such a change would still be consistent with the earliest divergence event in the *Anchomenus* clade; i.e., the basal divergence of *Tetraleucus picticornis* Newman, distributed in the eastern United States, from the rest of the group in Late Eocene (38 Ma). That event is still accountable to the most recent opening of the Atlantic Ocean (Noonan, 1986; Tangelder, 1988).

The Oligocene (38–25 Ma) would have seen range expansion of *Anchomenus* across the Palaearctic and into Vancouveran North America, as the Turgai Straits closed at 30 Ma uniting Asia-America with Europe (Noonan, 1986). The diversification of Old World *Anchomenus* starting in Early Miocene, as presented here, establishes Late Oligocene vicariance across Beringia between the ancestors of the present-day Old World and New World lineages within the genus. Tangelder (1988) also hypothesized initial Oligocene aged trans-Beringean vicariance within the *dorsalis* species group of the crane fly genus *Nephrotoma* (Diptera: Tipulidae), though later Pliocene and Pleistocene trans-Beringean relationships are also in evidence for this group. Allen (1983), reviewing relationships in a number of temperate forest arthropod taxa, found that Oligocene vicariance across Beringia was supported by taxon-area relationships in five of the nine taxa he studied, with the other four taxa uninformative on this issue.

In Liebherr (1991, fig. 378), I hypothesized Miocene vicariance as the agent causing divergence of *Elliptoleus* and *Sericoda*, those two genera comprising the adelphotaxon of *Anchomenus*. The Oligocene date of origin, hypothesized above, for ancestral *Anchomenus* suggests the time of divergence of *Sericoda* and *Elliptoleus* may be earlier than Miocene, constrained only by the origin of ancestral *Anchomenus* during the Oligocene (38–25 Ma). This suggests that the Mexican *Elliptoleus* may have started diversifying contemporaneously with the initial Oligocene formation of the Sierra Transvolcanica (Halffter, 1987). Such a conclusion allows taxa exhibiting Halffter's Nearctic Pattern to be as old as Oligocene, and not restricted to Plio-Pleistocene invasion of Mexico as he initially suggested (Halffter, 1976).

TAXONOMIC TREATMENT

The following couplets should be inserted into the Key to Adults of the *Anchomenus* Clade (Liebherr, 1991, pp. 26–30), allowing identification of *A. kurnakovi* and *A. punctibasis*. Figures mentioned with a capitalized legend are in this paper, those noted with lowercase are in Liebherr (1991). Parenthetical pages numbers following species names refer to Liebherr (1991).

ADDITION TO KEY TO ADULTS

6(5). Pronotum very evidently punctate (fig. 124, Fig. 9); elytral striae with closely set, regular, and coarse punctures 6a
6′. Pronotal punctures much fainter, aligned in transverse rows (fig. 125); elytral striae with indistinct and irregular punctures .... *Anchomenus yukihikoi* (p. 46)
6a(6). Upper body surface brunneous, legs testaceous; pronotum strongly cordate, laterobasal margins strongly concave, hind angles prominent (Fig. 124) .... *Anchomenus leucopus* (p. 45)
6a′. Upper body surface and legs dark; pronotum with laterobasal margins straight before denticulate hind angles (Fig. 10) .... *Anchomenus punctibasis*
7(5). Profemora with 2–4 posteroventral setae (figs. 56–63) 8
7′. Profemora with 5–8 posteroventral setae (fig. 55) 7a
7a(7). Mesofemora with 3 anteroventral setae (Fig. 11) .... *Anchomenus kurnakovi*
7a′. Mesofemora with 6–10 anteroventral setae (fig. 64) .... *Anchomenus dohrnii* (p. 37)

DESCRIPTIONS

Anchomenus kurnakovi (Kryzhanovskij), **New Combination**

Agonum (? *Anchodemus*) *kurnakovi* Kryzhanovskij, Kryzhanovskij and Abdurakhmanov, 1983:529.

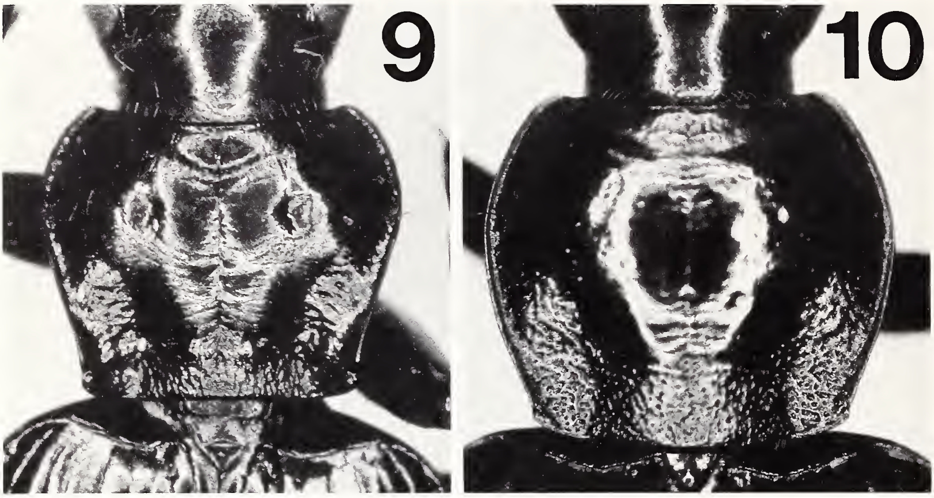
Diagnosis. Head above, pronotum, and elytra brilliant metallic blue-green; pronotal hind angles setose, thereby diagnosable from *A. cyaneus* Dejean; metathoracic flight wings reduced to vestigial flaps; metacoxae trisetose, inner seta present.

Description. Dorsal body surface metallic blue with green reflection; femora and ventral body surface piceous; tibiae, tarsi, mouthparts, and antennae slightly paler, brunneous. Eyes small in diameter but convex, ocular ratio 1.45. Pronotum cordate, laterobasal margins sinuate, strongly elevated outside wrinkled laterobasal depressions (Fig. 9); pronotal disc with well-developed impressions each side of midline;

Fig. 8. *Anchomenus kurnakovi* paratype ♂.

anterior transverse impression well-defined, discal area anterad impression depressed. Elytra flattened dorsally, lateral margins laterally explanate (Fig. 8); elytral intervals moderately convex; elytral striae nearly smooth, only faint indications of punctures in basal half. Three dorsal elytral setae and 18 lateral elytral setae. Metepisternum foreshortened, mesal margin 1.15× length of anterior margin; flight wings reduced to vestigial flaps. Profemur with 2–3 anteroventral setae and 6–8 posteroventral setae. Mesocoxa with 1 ridge seta; mesofemur with 3 anteroventral setae. Metacoxa trisetose, the inner seta present. Metafemur with 3 anteroventral setae. Fourth metatarsomere with inner and outer subapical setae. Fifth metatarsomere with 6 long ventral setae. Male abdomen with 1 apical seta each side.

Head with shallow isodiametric mesh microsculpture. Pronotal disc with transversely stretched isodiametric to transverse mesh microsculpture. Elytra with well-developed and slightly transversely stretched isodiametric mesh microsculpture (observed on ♂ paratype).



Figs. 9, 10. Pronota of *Anchomenus*. 9. *A. kurnakovi*. 10. *A. punctibasis*.

Standardized body length 7.8–8.0 mm (from Kryzhanovskij and Abdurakhmanov, 1983).

Male genitalia. Parameres basally melanistic, apically testaceous. Aedeagal median lobe with bluntly rounded apex (Fig. 12), lobe straighter near middle of length than closer to apex.

Types. Holotype ♀ (ASSP): Georgia, Adzharo-Imeritinsky mountains, north slope, upper Supsa R., 21-VI-1958, B. Kurnakov (not seen). Paratype ♂ (ASSP: incorrectly noted as female in Kryzhanovskij and Abdurakhmanov [1983]) with same data (specimen was examined).

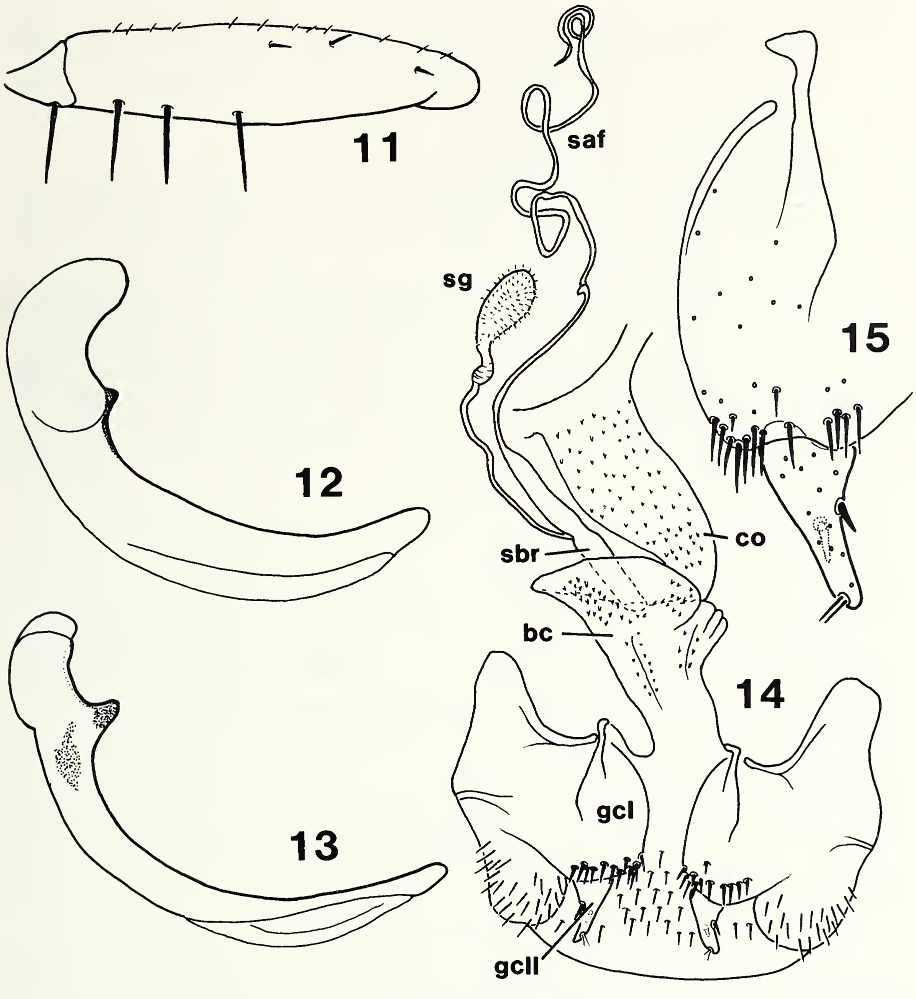
Distributional range. Known only from the types collected in the Georgian mountains (Fig. 3).

Anchomenus punctibasis (Reitter), **New Combination**

Agonum punctibasis Reitter, 1894:123.

Diagnosis. Body and legs uniformly piceous; pronotum with denticulate hind angles, convex laterobasal margins, and densely punctate laterobasal depressions and median basal area (Fig. 10); discal elytral striae strongly punctate in basal half; 6–8 anteroventral setae on mesofemur.

Description. Eyes large and convex, ocular ratio 1.80. Pronotum with convex laterobasal margins before the denticulate hind angles (Fig. 10); laterobasal depressions shallow; pronotum densely punctate across base and forward laterally to one-half of length. Elytral intervals convex; elytral striae strongly and regularly punctate in basal half, especially on disc, weakly punctate in apical half of elytron. Three dorsal elytral setae and 16–17 lateral elytral setae. Metepisternum elongate, flight wings fully developed. Profemur with 8–10 anteroventral setae and 6 posteroventral



Figs. 11–15. 11. Left mesofemur, *Anchomenus kurnakovi*, ventral view. 12, 13. Aedeagal median lobe, right side view (ventral side in repose). 12. *A. kurnakovi*. 13. *A. punctibasis*. 14, 15. Female reproductive tract structures of *A. punctibasis*. 14. Female reproductive tract, ventral view. 15. Enlarged ventral view of left gonocoxa. bc = bursa copulatrix, co = common oviduct, gcI = basal gonocoxite, gcII = apical gonocoxite, saf = spermathecal apical filament, sbr = spermathecal basal reservoir, sg = spermathecal gland.

setae. Mesocoxa with 4–5 ridge setae; mesofemur with 7–8 anteroventral setae, 5 setae on dorsal half of anterior surface, plus 15–17 setae in a row along dorsal surface. Metacoxa trisetose, inner seta present; metafemur with 6 anteroventral setae. Fourth metatarsomere with inner and outer subapical setae; fifth metatarsomere with 6 ventral setae subequal to width of tarsomere at points of insertion. Abdomen with 2 setae each side at apex in females, 1 seta each side in males.

Head with well-developed isodiametric mesh microsculpture on neck, vertex shinier with weak microsculpture. Pronotal disc with shallow transverse mesh microsculpture, median base with irregular transverse mesh, laterobasal depressions with more evident, transversely stretched isodiametric sculpticells. Elytral intervals with granulate isodiametric microsculpture.

Standardized body length 8.5–9.3 mm.

Male genitalia. Parameres basally melanistic, apically brunneous. Aedeagal median lobe narrow throughout length, apex tightly rounded (Fig. 13); shaft slightly darker at parameral articulation, testaceous apically.

Female reproductive tract. Penultimate gonocoxite with apical fringe of 12–13 larger setae (Figs. 14, 15), with 1–2 smaller setae slightly basad apical fringe (Fig. 15). Apical gonocoxite with 1–2 lateral ensiform setae, 1 dorsal ensiform seta, and 2 nematiform setae in apical depression. Bursa copulatrix with lumenal microtrichia, densest and longest near entrance of spermatheca and common oviduct (Fig. 14); common oviduct with well-developed lumenal microtrichia. Spermatheca with basal reservoir and apical filament about 3 × length of reservoir. Spermathecal gland duct entering about middle of length of basal reservoir.

Type. Described from more than one specimen from the Sefir-Kuh (now Safid Kuh) mountains north of Herat, Afghanistan, based on Reitter (1894) considering the length of specimens to be 9–10 mm. The types could not be located in the Reitter collection, Hungarian Natural History Museum, Budapest (G. Szél, pers. comm.). I have based the identification on the 2 Hauser specimens (MNHB) from Oasis Tedzhen (Apfelbeck collection, determined by A. Jedlička, confirmed by J. Schmidt, Rostock). Tedzhen is approximately 300 km from the type locality.

Distributional range. Found in Transcaspia, from Turkmenistan and Iran east to Tadzhikistan. Also known from in the Abkhazian region of the Caucasus (Fig. 3).

Material examined. GEORGIA: Abchasien [= Abkhazia] (ZSSM, 2). IRAN: Aliabad, V-1967 (DMMC, 1); Chaldée Persane, Kélateh = [Qalat], 300 m, 1904 (MNHP, 1); Zabol, Berang, V-1950 (DMMC, 1). TADZHIKSTAN: Dushanbe Prov., Nishni Piandsh, VI-1986 (DMMC, 3). TURKMENISTAN: Oasis Tedzhen, VIII-1903 (BPBM, 6; MNHB, 2).

Nomenclatural note: There remains potential confusion concerning the synonymy of *Anchomenus punctibasis*. Specimens at Budapest of the Tedzhen series collected by Hauser have been considered *A. punctibasis* Reitter by Jedlička and Schmidt. The Bishop Museum's portion of the series was determined as *Anchomenus turkestanicus* Ballion (1871) by an unknown determiner. This name is based on specimens from Khodzhent, Tadzhikistan, with the type deposited in Ballion's collection, now at the University of Odessa, Ukraine (O. L. Kryzhanovskij, pers. comm.). This type was unavailable to me, and Ballion's description is inadequate for identification. Therefore, I cannot evaluate this potential synonymy.

ACKNOWLEDGMENTS

I thank O. L. Kryzhanovskij, Russian Academy of Sciences, St. Petersburg, for making possible the loan of *A. kurnakovi*, and for much helpful information on Russian collections. I also thank J. Schmidt, Rostock, Germany, for information on Palaearctic Platynini, and P.

Oosterbroek for helpful criticism of the manuscript. This research was partially supported by Hatch project NY(C)139406, and the National Science Foundation (BSR-8614628).

LITERATURE CITED

Allen, R. T. 1983. Distribution patterns among arthropods of the north temperate deciduous forest biota. Ann. Missouri Bot. Gard. 70:616–628.

Ax, P. 1987. The Phylogenetic System. John Wiley & Sons, Chichester. xiii + 340 pp.

Ballion, E. 1871. Eine centurie neuer Käfer aus der Fauna des russischen Reiches. Bull. Soc. Imp. Nat. Moscou 43(2):320–359.

Brown, W. L., Jr. 1957. Centrifugal speciation. Quart. Rev. Biol. 32:247–277.

Farris, J. S. 1988. HENNIG, HENNIG86 Reference, Version 1.5 [A Computer Program for Cladistic Analysis]. Port Jefferson Station, N.Y.

Frenzel, B. 1968. The Pleistocene vegetation of northern Eurasia. Science 161:637–649.

Halffter, G. 1976. Distribution de los insectos en la zona de transicion Mexicana, relaciones con la entomofauna de Norteamerica. Fol. Ent. Mexicana no. 35:64 pp.

Halffter, G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. Ann. Rev. Ent. 32:95–114.

Kryzhanovskij, O. L. and G. M. Abdurakhmanov. 1983. New and little known species of supertribe Pterostichitae (Coleoptera, Carabidae) from the Caucasus. [In Russian] Rev. Ent. U.R.S.S. 62:529–531.

Liebherr, J. K. 1991. Phylogeny and revision of the *Anchomenus* clade: the genera *Tetraleucus*, *Anchomenus*, *Sericoda*, and *Elliptoleus* (Coleoptera: Carabidae: Platynini). Bull. Am. Mus. Nat. Hist. no. 202:163 pp.

Maddison, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Syst. Zool. 40:315–328.

Noonan, G. R. 1986. Distribution of insects in the northern hemisphere: continental drift and epicontinental seas. Bull. Ent. Soc. Am. 32:80–84.

Oosterbroek, P. and J. W. Arntzen. 1992. Area-cladograms of circum-Mediterranean taxa in relation to Mediterranean palaeogeography. J. Biogeogr. 19:3–20.

Page, R. D. 1989. COMPONENT, Release 1.5 [A Computer Program for Cladistic Biogeography and Component Analysis]. Auckland, New Zealand.

Page, R. D. 1990. Component analysis: a valiant failure? Cladistics 6:119–136.

Plaziat, J.-C. 1981. Late Cretaceous to Late Eocene palaeogeographic evolution of southwest Europe. Palaeogeogr., Palaeoclimatol., Palaeoecol. 36:263–320.

Reitter, E. 1894. Zehnter Beitrag zur Coleopteren-Fauna des russischen Reiches. Wien. Ent. Zeit. 13:122–128.

Steininger, F. F. and F. Rögl. 1984. Paleogeography and palinspastic reconstruction of the Neogene of the Mediterranean and Paratethys. Pages 659–668 *in:* J. E. Dixon and A. H. F. Robertson (eds.), The Geological Evolution of the Eastern Mediterranean. The Geological Society, Blackwell Scientific Publications, Oxford.

Tangelder, I. R. M. 1988. The biogeography of the Holarctic *Nephrotoma dorsalis* species-group (Diptera, Tipulidae). Beaufortia 38(1):35 pp.

Received 21 June 1993; accepted 19 January 1994.